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"................. per litora spargite muscum,
Naiades, et circùm vitreos considite fontes:
Pollice virgineo teneros hìc carpite flores:
Floribus et pictum, divæ, replete canistrum.
At vos, o Nymphæ Craterides, ite sub undas;
Ite, recurvato variata corallia trunco
Vellite muscosis e rupibus, et mihi conchas
Ferte, Deæ pelagi, et pingui conchylia succo."
N. Parthenii Giannettasi, Ecl. 1.

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I.—*The Prototheca of the Madreporaria, with Special Reference to the Genera* Calostylis, *Linds., and* Moseleya, *Quelch.* By Henry M. Bernard, M.A. Cantab., F.L.S.

[Plate I.]

The task I have set myself is to sketch what appears to have been the leading features in the evolution of the Madreporarian skeleton. The researches on which the arguments are based have been almost entirely limited to the skeleton, not because the importance of a close study of the soft parts is not recognized, but because, for the attainment of accurate results, the widest possible survey of homologous structures is indispensable. This condition can never be supplied by the soft parts. They can at the most be studied in a few recent specimens, whereas the vast majority of the forms presented by the Madreporarian system are fossil. Further, let me add in passing that I do not believe that the study of the individual development of a few living forms can by itself establish anything certain about the past history of the group, for the simple reason that we cannot tell whether any special developmental feature is a repetition of some ancient condition or a recent adaptation *. As I have already often maintained, lines of phylogenetic growth can only be satisfactorily established by the discovery of connected series of variations, morphologically and chronologically arranged. The skeleton alone can supply us with such series, and that of the corals probably with a more complete series of forms, extending *from the Palæozoic era to the present day, than will ever be obtained of any other animal group.* Whether, therefore, the skeleton be of great or of little importance in itself in the morphology of the corals, it alone supplies us with what we want—a continuous series of homologous structures. On this account alone, then, when our aim is taken into account, we are obliged to confine our attention to the skeleton.

As a matter of fact, the skeleton is of paramount importance in the coral organism. There is a sameness in all the soft parts which limits their morphological importance in any comparative study. Their chief variations may, for practical purposes, be said to be repetitions of the variations of the skeleton which they secrete. The skeleton is, *par excellence*, the chief structural feature of the coral, its relation to the soft parts being extremely simple. It is, as we now know, thanks to the researches of von Koch, Heider, Fowler, Bourne, Ortmann, and Miss Ogilvie, an excretion of the basal parts of the outer wall of the body, and hence morphologically it is external to the organism. At times very complicated, it is an organ of protection and support for the body of the polyp, or, in colony formation, for the colonies of polyps, the polyps themselves, thus protected, having, as a rule, remained simple and primitive. The corals, indeed, present us with a group of organisms still primitive enough to illustrate the fact that, of the earliest morphological modifications of the living matter, skeletal formations were the most pronounced. This is strikingly exemplified by the Foraminifera and Radiolaria, in which there is a wealth of skeletal formations with little or no visible variation of the soft matter. Again, in the sponges the skeletal variations far outrun those of the soft parts. The same is true of the stony corals.

In what follows, therefore, I shall make no detailed reference to the soft parts or to the excellent work which is being done with their help by Dr. Duerden towards the elucidation

* N. Guldberg and Nansen, "On the Development and Structure of the Whale," Bergens Museum, 1894, p. 39; also Sedgwick, Proc. Fourth International Congress of Zoology, 1898, p. 74.

of the same problem as that which here interests us. I shall confine myself solely to showing how some of the chief transformations of the skeleton can be linked into series and how, in a few cases, the causes which led to those transformations are apparent. We are justified in hoping that the conclusions obtained from the continued studies of the soft parts on the one hand and of the skeleton on the other will ultimately coincide.

I wish to make it specially clear that only a few of the lines of modification can be dealt with, but those few, being some of the earliest, are, I believe, the most fundamental and important for the elucidation of all the later transformations of the coral skeleton. To deal with the whole of these latter would be to write a complete systematic account of the stony corals. This is the aim of the great catalogue now being prepared and published by order of the Trustees of the British Museum, and must be a work of years *.

The researches of the writer in reference to this work so far hardly entitle him to speak with confidence on any other of the larger divisions than the Perforata; no other has as yet been systematically dealt with by him, at least in the thorough manner required for a British Museum Catalogue. It would not, however, have been possible to discover the morphology of these highly specialized Perforate forms without a study of and constant reference backwards to earlier and simpler types. In this way certain lines along which the stony corals have travelled, viz., those leading from the most primitive to the most specialized, have been growing clearer.

* The last attempt to deal with the whole of the coral system in the 'Hist. Nat. des Coralliaires' of Milne-Edwards and Haime, completed in 1860 by Milne-Edwards alone, was founded on comparatively small collections and written at a time when the relations between the skeleton and the polyps were not understood. The excellence of the results which were nevertheless obtained is, on the one hand, a tribute to the genius of the great French naturalists, and, on the other, a witness to the comparative unimportance of the polyp, morphologically, as compared with the skeleton.

The new catalogue projected by the authorities of the British Museum, and rendered necessary by the immense increase in the collections due especially to the sending out of scientific expeditions, was started in 1876, but was interrupted by the death of Dr. Brüggemann, who was engaged for the purpose. After fourteen years Mr. George Brook undertook the work, but again death intervened soon after the first volume was published in 1893. Two years were again lost, when the present writer was appointed to continue the work. There are now four volumes published, and the fifth is rapidly approaching completion. Each volume is practically a monograph of one, or at the most two, genera, and, like the earlier attempt of Milne-Edwards and Haime, it now describes the fossil as well as the recent forms.

The following pages sum up the principal conclusions he has arrived at.

The most important stage to establish in an evolutionary history is the first, or that which we may consider as the first, inasmuch as from it all the modifications we wish to compare can be deduced. The first stage in the evolution of the coral skeleton was first dimly recognized by me in the minute *saucer*-shaped cups of young Madreporidan colonies—so young as to consist only of a parent calicle and one or two daughters. In none of the Madreporids have I yet found the earliest stage in which the cup containing the parent alone was *cup*-shaped. Such a stage, however, may be legitimately assumed.

The discovery of such colonies made three points clear to me:—

1. The parent calicle of a colony rises out of a basal cup—the PROTOTHECA *.

2. This prototheca is not a composite structure, but a morphological unit, the rim of which can be bent up, flattened completely down, and indefinitely expanded in any direction as a film, from the upper surface of which, as originally from within the cup, the coral skeleton arises.

3. This film is the EPITHECA †.

These conclusions received complete confirmation from a study of the Palæozoic form *Favosites* and of its modern descendant *Alveopora*. I have already described and figured the prototheca of the latter genus ‡. Its rim, as shown in the figures referred to, does not usually flatten down, but grows upwards and outwards to form the irregular film-like investments characteristic of the colonies of this genus.

In both cases—that is, in Madreporidæ and Favositidæ alike—it was easy to see the bars of the intracalicular skeleton rising directly out of the wall of the cup as internal projections from its surface; this point is of importance, because von Koch, whose developmental researches also revealed to him the prototheca, was led by what he saw to regard it as a composite structure consisting of a *basal portion* ("Basal-

* Lindström suggested the word "initium" for the earliest cup-like skeleton; the term "prototheca" was suggested to me in conversation by my friend Prof. Jeffrey Bell.

† The fact that the skeletal elements rise from the surface of the epitheca was pointed out by Martin Duncan in 1884 (Journ. Linn. Soc., Zool. xvii. p. 361) as indicating the importance of that element of the coral skeleton.

‡ Journ. Linn. Soc., Zool. xxvi. 1898, p. 495, pl. xxxiii.

platte," sole) and of a peripheral portion (*epitheca*). This appears, however, now to have been a too literal rendering of the facts of his observations, for no one who had seen several of these epithecal saucers of different sizes and with edges turned up to different heights at different curves, and the skeletal bars springing indifferently from the sides and the base, could possibly divide it into a basal and a peripheral portion.

Besides, in a young saucer-shaped colony it is obvious that the turned-down side (the "epitheca") of the parent becomes the "basal plate" of the daughter, and in this successive flattening down of the rim we can see the explanation of the characteristic wrinkled appearance of the supporting epitheca of so many horizontally expanding corals, whether single or compound. Each furrow represents a pause in the outward growth long enough to allow the rim of the widening saucer-shaped epitheca to grow upwards a short distance. The next period of growth carries it downwards and outwards again. This process has been actually seen by Lacaze-Duthiers * in the development of *Balanophyllia regia*. This writer observed three attempts of the basal secretion of the larva to turn up to form a cup or "envelope calicinale," but they were always futile; the septa overran them and the edge was flattened down again and continued as a basal secretion (*cf.* Pl. I. fig. 10).

Before continuing with the history of this prototheca—that is, with our account of some of its earliest modifications—it will strengthen our argument to mention a few instances in which earlier writers have come near to recognizing this identity of the prototheca with the epitheca. As we might expect, such an identification would be more probable in relation to Palæozoic forms, in which the primitive cup remained longest in evidence and had not become so distorted and masked as it is in the majority of the modern forms. Milne-Edwards †, in describing the Palæozoic genus *Zaphrentis*, which, from its appearance in time, might have been expected to have retained the prototheca, says that it is completely surrounded by an epitheca. Nicholson could not distinguish the epitheca of these same corals from the wall. Miss Ogilvie ‡ declared that in *Zaphrentis* the epitheca "supplied the primitive base and periphery in one," and again that the primitive wall of corals was epithecate; and

* Arch. Zool. expérimentale, (3) vol. v. 1897, pp. 179–183 & 230, pl. x. figs. 19–24.

† 'Les Coralliaires,' iii. p. 335 (1860).

‡ Phil. Trans. 1896, p. 320 &c.

again the same writer recognized the wall of *Zaphrentis* as "euthecate," which means that the persistent prototheca in these early corals is the eutheca or true primitive wall of Heider and Ortmann, as compared with which all other thecæ are secondary. To this last opinion we shall return.

Mention should also surely be made of Ludwig *, who, so long ago as 1866, attempted to found a classification upon his recognition of the prototheca as the primitive shell ("Gehäuse") of the coral polyp. But beyond the interest attaching to the fact that he thus emphasized the importance of the prototheca in Madreporarian morphology his work has no value, for he was led astray in his further analysis by a fancied analogy with the shell of the mollusk.

In the present paper, then, we start again from the recognition of the prototheca, but this time, avoiding Ludwig's mistake, we shall try to analyze some of the actual modifications which this primitive coral skeleton has undergone in the progress of its evolution. So far from being as simple as Ludwig appears to have assumed it to be, it is a task of considerable complexity to follow and of no small difficulty to describe. This paper, indeed, was begun five years ago, and has been frequently rewritten.

As I have shown, those parts of the coral skeleton called epitheca must for the future be referred to the rim of the prototheca. This seems simple and clear now, but in the past the epitheca has been *the* stumbling-block of coral morphology. It has been this for the very reason that it waited for the discovery of the prototheca before there was any possibility of its elucidation. The fact of the confusion in the prevailing views as to what the epitheca is is familiar to every coral student. For instance, Prof. Gregory, of Melbourne, after all his years of work at corals, characteristically summed up his despair of ever making anything out of it by declaring that "there was no part of the coral skeleton over which more time had been wasted" †. This attitude and that which is taken in this paper are poles asunder. Between these two, authors and text-books hover. None are so bold as Prof. Gregory, yet none have succeeded in formulating an intelligible doctrine.

We may here state that there is ample excuse for this confusion, for even now that we know that the epitheca, as it occurs in the majority of specimens, is only an extension of the rim of the original cup, still in each case the problem as

* 'Palæontographica,' vol. xiv.

† Palæontol. Indica, ser. IX. vol. ii. p. 11 (1900).

to how this can be requires unravelling. It may, for instance, be the rim extended indefinitely and continuously as a chalky film round a colony (e. g. *Alveopora*), or, again, it may be discontinuous and represent the separate rims of an aggregation of corals, each with its own cup, as in so many Palæozoic forms. In this case it depends upon the way in which the corals are aggregated whether the rims are easy or difficult to recognize. Add to these difficulties the fact that apparently any part of the surface of a polyp may die down and secrete a calcareous film * which is purely adventitious and has no morphological significance, and it is obvious that until we had a key to its elucidation the epitheca could not fail to be a source of bewilderment.

Diagram 1 (Pl. I.) shows the three earliest growth periods of a primitive Madreporarian skeleton. All that we see is a deep cup with three tabular floors. The process is explained in diagram 2, in which we see three cups progressively modifying their shapes. The lowest of these is the prototheca in the strict sense of the word †, but it is advisable to apply the term to all simple repetitions with free edges. Fig. 2 is so far diagrammatic, inasmuch as with cups of this shape it is impossible to say how far the rim of each cup extended before the soft parts of the base of the polyp became detached from the base of its prototheca. Cases, however, do occur in which the change in the shape of the new thecæ was rapid, and for this and also for other reasons the rims of the separate

* The formation of calcareous films somewhat irregularly over the skin of corals is hardly to be wondered at. The prototheca was but the primitive secretion of the basal portion of the polyp, forming a protective cup into which the animal could retract the oral and exposed end of its body. Above the rim of this cup calcareous secretions were not usual, otherwise they would have interfered with the process of retraction, but the power of secreting them was not lost. Indeed, some forms actually secreted lids, which, when the polyps retracted, closed down over the prototheca (*Calceola*, *Goniophyllum*). A histological difference between these secondary films and true epitheca may sometimes be noticed. The former may be built up of separate plates, each of which starts round some point of the skeleton and grows by concentric increments.

† The prototheca is here drawn quite diagrammatically. Figure 8, after Lacaze-Duthiers, is one of the best figures from life. My own figures, already referred to, of a young *Alveopora* are of a prototheca somewhat distorted. Theoretically we might expect a slight constriction above the flattened sac, for as the soft larva settled down we might expect its aboral end to flatten out somewhat wider than the neck carrying the oral disk and tentacles. The base of the second prototheca might easily be rounded or pointed, for it would hang down in the hollow of the prototheca proper. The later development of *convex* tabulæ and vesicular dissepiments may have been due to the pulls of mesenterial muscles.

cups may be distinguishable. For instance, the development of exsert laminate septa may lift the cups above one another (see Pl. I. figs. 3, 11, 12).

Fig. 3 refers to *Montlivaltia*, of especial interest because it was the irregular bands of epitheca round specimens of this genus which induced Dr. Gregory to give up this element of the coral skeleton in despair. We shall now show that an understanding of these bands is essential to a true insight into the morphology of the skeleton.

It is frequently stated * that in *Montlivaltia* there is epitheca, but no theca. There was, however, certainly a prototheca, and examination of the coral shows that the successive protothecæ gradually flattened out until, after reaching a certain size, they formed a series of flat saucers (fig. 3, *e*, *e*, *e* . . .) of nearly uniform size, and piled up one above the other as tabulæ with edges which may either only just reach the surface or be bent sharply upwards to varying heights according to the accidents of secretion. On the left of the figure a few of the septa are shown supporting and raising the successive saucers above one another. The septa of each polyp continue those of that which went before it, so that these radial structures naturally run up continuously through the whole skeleton. On the left of the diagram the saucers alone are shown in optical section as a series of flat or wavy floors with turned-up rims.

Here, then, we have the three facts necessary for the understanding of the case in hand:—

1. A series of shallow thecæ or protothecal saucers ending abruptly at the surface or with edges bent up externally.

2. The septa which, being exsert, support and lift these saucers above one another, so that, while the septa are continuous, the rims of the cups may be free and separate, or, when bent up, may run together as irregular epithecal bands.

3. The extreme irregularity of the bands is due to the want of uniformity in the height to which the secretion of the rims of the saucers, if bent up, extends.

These three factors fully explain the puzzle presented by the epitheca of *Montlivaltia*.

It is obvious that in diagram fig. 3 the saucers might contain not single polyps, but gradually expanding colonies

* *E. g.*, by Miss Ogilvie (*l. c.* p. 158), who, however, followed Milne-Edwards and Haime, who wrote with reference to *Amplexus*, in which the succession of saucer-shaped protothecæ is very pronounced:—"Quelquefois même la muraille paraît manquer et le polypier n'est constitué que par une série de cornets très évasés et naissant les uns au-dessus des autres" (Ann. Sci. nat. (3[e]) ix. p. 84, 1848).

(*cf.* the minute colonies of Madreporids already mentioned). Such series of gradually expanding colonies might grow into columnar or massive stocks widening at the top. In all such stocks the tabulæ which run through them must be regarded as the floors of successive saucers. This is well exemplified in the genus *Goniopora,* as I have already explained *. In this genus too we have, as we have in *Montlivaltia,* irregular bands of epitheca running round the stocks. These are the rims of the protothecal saucers showing irregularly at the surface. In *Alveopora* the rims all run together to form continuous epithecal investments, except, perhaps, in their branching forms, in which the protothecæ may be lifted up above one another by the growth of the spiny septal skeleton.

For an understanding of the morphology of the coral skeleton we must bear in mind that essentially the same process, viz. *a succession of epithecal cups or saucers, occurs throughout the whole of the Madreporaria.* They may be simple conical cups fitted one into the other (*Zaphrentis*) or flat plates piled up (*Montlivaltia, Goniopora*), or their epithecal floors may be thrown into complicated folds and both the cup and its repetitions may be difficult to unravel, but the fundamental principle is the same throughout. There is only one group I can think of in which the epitheca is not normally repeated, namely in the highest Madreporids—*Madrepora, Turbinaria, Montipora, Astræopora,* and their simpler ancestors the Eupsammiids. In these the purely septal skeleton rises rapidly above the original flattened prototheca which is then left behind. This is the reason of that well-known characteristic of these forms that the calicle cavities run continuously for long distances through the skeleton.

We repeat, then, for the sake of emphasis that wherever the epitheca occurs it represents the rim or the coalesced rims of one or more protothecal cups or saucers, the floors of which are represented by the tabulæ. In any individual case the tabula below the living layer is the nth repetition of the original prototheca of the parent polyp.

The main problem, then, of the student of coral morphology, that is, taking the skeleton alone into account, is to trace the various modifications of the prototheca from its earliest simple cup stage to the many different shapes and positions it now assumes and occupies as part of the coral skeleton.

Roughly speaking, we may say that there are two periods in the evolution of the Madreporaria—that in which the prototheca, though modified, remains in evidence, and that in

* *Cf.* vol. iv. Brit. Mus. Madreporaria, p. 24, diagram A.

which it has disappeared from view or is difficult to unravel. Only in the few Madreporids (the chief families of the Perforata) above mentioned can it be said to have been aborted, and then only in a limited sense, for the whole coral skeleton is its product. If the original rim of the cup is replaced as the edge of the theca by new thecæ formed either by the rising up of concentric folds from its floor or of radial plates from its sides, or by complicated combinations of these two, these new thecæ are strictly infoldings of the prototheca. The prototheca, then, however obscured its early cup shape, being replaced by secondary cups produced by its own infoldings, remains throughout *the fundamental element in the Madreporarian skeleton.*

I propose here to trace some of the more obvious transformations of the prototheca, treating them entirely morphologically—that is, simply as forms which admit of explanation and deduction from simpler forms, and without regard to their real phylogenetic sequences.

The working out of these latter—that is, the attempt to discover the real places of these transformatory processes in the genealogy of the Madreporaria—must be a work of time. I am convinced, however, that it will at once give a new and much needed interest to the student of the stony corals.

We return, then, to our simplest form (diagram fig. 1). It shows us a conical cup standing on a flattened slightly expanded base and gradually thickening upwards. *The problem of increasing instability must obviously have been one of the first which the polyp inhabiting such a skeleton had to solve.* I shall endeavour to show that the earliest divisions of the Madreporaria were due to the different ways in which this problem was solved.

I. *Falling over and recovery of the upright position.*—The simplest of all methods was to fall over so that the flesh of the polyp could come once more into contact with the substratum and secrete a new cementing layer where it touched. From this new base the polyp could bend upwards once more securely attached. The following is some of the evidence which shows that this actually took place:—

(*a*) The earliest period is specially characterized by the great number of single corals which are conical but curved. The curve is exactly what is required; that is, it is most pronounced at the tip, e. g. *Zaphrentis*, *Menophyllum*, &c.

(*b*) All these curved corals have what is known as a fossula, that is a deep depression within the calicle and most frequently on the convex or what is called the "dorsal" side. The fossula has a very simple explanation, if the assumption of the falling over is correct (see diagram fig. 4). As the soft parts detach themselves from the base of the prototheca they might be expected to bag down, and they will continue to be acted upon by gravitation and drawn over towards the convex side of the coral until the vertical position has been regained. It is possible that this bearing over to the side may be due to the efforts of the polyp itself to bend up, but gravitation is a *causa efficiens.*

In some forms, however, the fossula is not on the dorsal, but on the ventral side. There is abundance of scope for variations of all kinds: a deep cup (that is, the cup of a polyp which grew very slowly in width, for instance) would lie very prone and its fossula would fall over to the dorsal side (diagram fig. 4); but a shallower more open prototheca (that is, one in which the polyp grew very rapidly in width) would, in the prone position, have one (the "ventral") wall nearer the vertical, and this would keep the skin of the point while it hung loose for the while near the ventral side, and the fossula would consequently also appear on this side (diagram fig. 5) *.

(*c*) The falling over of the prototheca will explain the departure from a strictly radial symmetry of the septa seen in these curved Palæozoic corals. It is obvious that, as the coral is bending to the vertical, seen from above, the septa would have the arrangement shown in diagram fig. 6, which is after the classical figure of Kunth showing the septal formula typical of the group called Rugosa. The position of the fossula with relation to this modification of the septal arrangement shows that this is the true explanation. Further, it has long been known that, as such corals gradually reacquire a vertical position, the septal arrangement slowly gives up the bilateral and returns to the radial symmetry. Thus the character on which it was proposed to found a great division of the stony corals was nothing but a slight mechanical

* This is not the first time that this origin of the fossula as a repetition of the tip of the prototheca has been recognized. Ludwig's figures made it quite clear in 1866 ("Corallen aus paläolithischen Formationen," Palæontographica, xiv. 1866). But, regarding the skeletons as analogous to the shells of mollusks, to whose shapes he thought they were adapted, he failed entirely to understand the true character of the coral skeleton or of the causes of its changes.

The use assigned in text-books to the fossula, viz. as a sort of crypt for the sexual products, is probable enough, but need not have been the cause of its origin. I fail to see the evidences for the existence of more than one true fossula in any coral I have examined. Superficial irregularities in the septa, due perhaps to the presence of sexual products, may be quite distinct from the true fossula. A longitudinal section or a fracture showing a complete tabula is the only evidence which can be relied on.

adaptation to a passing phase in the life of each individual coral. But it is only fair to say that the whole tendency of recent works on corals has been to discover the invalidity of the supposed division Tetracorallia.

Into the interesting questions which this suggests as to the value of the existing divisions of the corals, we cannot here enter, but content ourselves with merely pointing out that while probably all the *very earliest* corals fell over and, if they bent up again, became Tetracorallia during the process, it is possible that many, which later had learnt a different method of acquiring stability, might easily be knocked over and in their efforts to become vertical again might become Tetracorallia by accident.

(*d*) The falling over of the prototheca enables us to find an origin for several groups which are usually regarded as corals, but whose position is still a matter of uncertainty. It is quite within the limits of probability that a certain number of these overturned polyps in their small protothecæ should remain prone and bud in this position. One such case we know of for certain (see p. 28, on *Heliolites*). We ask whether the creeping branching stocks of *Aulopora* might not also have been formed by the early budding of a parent whose prototheca had fallen over.

From *Aulopora* the genus *Syringopora* might be deduced. *Syringopora* is said to begin with the same horizontal creeping stock as *Aulopora*, and then to bend up and form its tufts of wavy tubes freely communicating with and supporting one another. In these erect tubes very irregular tabulæ are formed by the constant rising of the polyp in the tube as the latter lengthens. The very presence of tabulæ and of the rudimentary septa, consisting of rows of points, clearly indicates an affinity with early Madreporaria. Add to these the protothecal outer covering, and we have the same three structures which make up an *Alveopora* or a *Favosites*. It is only their dispositions and the relative developments of the parts which differ *.

Halysites could also be deduced from such a prone theca by rapid continuous budding, in such a way that the parent and its buds bent up in rapid succession into the vertical, as shown in the diagram fig. 7, each then continuing to grow as a thin flattened tube. These in contact and mutually supporting one another would supply the typical skeleton of this

* The apparent affinity between *Syringopora* and *Favosites* has been pointed out by Mr. Bourne (Phil. Trans. vol. 186 B, p. 474). But *Favosites* is structurally indistinguishable from *Alveopora*, and was not therefore an Alcyonarian (Proc. Linn. Soc., Zool. vol. xxvi. (1898) p. 495.

remarkable genus. We have the same three elements, protothecal tubes, tabulæ, and spiny septa *.

(*e*) The habit of falling over is known still to occur in the genus *Flabellum*.

(*f*) Lastly, I appeal to the modifications of the prototheca which will be described in the following pages, every one of which may be regarded as an adaptation for the purpose of solving the problem of vertical stability, that is, how to avoid the natural consequence of having to stand on a point while continuing to grow in height and bulk. For we are surely justified in assuming that the falling over at the very outset of life of an organism intended, if we may say so, to stand upright, would mean considerable loss of time and energy during the reattainment of the upright position. Such a loss might be expected to delay budding, and it is probable that we may have to take this into account in our ultimate classification. We may have to form a group which arose from the early budding of parents still in their protothecæ (*sens. str.*), and this would include such forms as *Aulopora*, *Syringopora*, and *Halysites*, in all of which the protothecæ fell over, and to these we might add *Chætetes* arising probably by fission. Whether the prototheca also fell over in this last case I have not ascertained. Such a group arising from parents still in their protothecæ proper, would stand in contrast to another group in which the budding was delayed until the polyp had grown considerably larger and had again assumed the upright position, and our divisions of these latter would have, in the first instance, to be based upon the methods adopted to attain this end.

II. *Radicle-formation.*—This process has been carefully studied and described in *Flabellum* by Lacaze-Duthiers †. A small portion of the lip of a prototheca bends over until it adheres to the ground (see diagram fig. 8 *a*, *b*). I have myself seen a similar process as an occasional thing in young colonies of *Alveopora*. It is difficult to see how the great pear-shaped colonies in this latter genus could possibly stand upon the tip of the original prototheca without gaining support on this principle. Extensive droopings of the rim till it touched the ground with subsequent bends up again are probably more common in this genus than the formation of thin radicles.

Root-processes may come from the rims of different protothecæ in those cases in which the corallum is built up of a

* *Cf.* Fischer-Benzon, Abhandl. wissench. Ver. Hamburg, Bd. v. 2 (1871), pp. 1–23.

† Arch. Zool. expér. (3) ii. 1894, p. 445, pl. xviii.

series, like those shown, for instance, in fig. 3. *Omphyma* is a typical case.

But this whole process need not detain us; it has no serious morphological value, being obviously a device for a certain end. When that is attained, it has no further influence on the shape of the skeleton *.

III. *Early flattening out of the Prototheca.*—It is obvious that if, by any means, the early prototheca could be transformed rapidly into a disk, a broad base could be acquired by the skeleton which would keep it upright. It seems to me clear that the morphology of many of the Palæozoic corals can be explained on this hypothesis. But the different ways adopted of so changing the primitive conical prototheca seem to have been very numerous, and a review of the forms from this point of view is a desideratum. It is, I believe, along this line that we shall find a more natural set of characters for the revision of such groups as those now included, *e. g.*, in the Cyathophyllidæ, than any now adopted.

In the present place I can only give a few samples, and, to avoid doubt as to the forms meant, I propose to take as examples certain well-known figures accessible to every student.

"*Zaphrentis gigantea*," pl. iv. of Milne-Edwards and Haimes's Pol. foss. d. Terr. paléozoïques. I give this in passing because it is interesting as a very irregular method of acquiring a broad flat base. Diagram fig. 9 (Pl. I.) shows my interpretation of the process. It may be that the coral did not actually become detached and fall over, but that the method may be compared with radicle-formation, only, instead of a narrow lip, the whole side of the prototheca bent outwards and apparently became cemented to the substratum.

It will be seen from a comparison with Milne-Edwards and Haimes's figures that in this diagram I am assuming what the early transformation of the prototheca was from the shape of the tabulæ in the adult stages; and this is, I believe, perfectly justifiable. Unfortunately not sufficient attention has yet been paid to the variations of the prototheca, which are still to be discovered. In certain types of modifications, *e. g.* those shown in diagrams figs. 11 and 12, the very earliest

* Miss Ogilvie's suggested origin of the Perforata from a great elaboration of root-processes so as to form the reticular cœnenchyma is very ingenious. But it is hardly borne out by the development of young Madreporidan corals in which the cup- or saucer-shaped prototheca persists as a basal epitheca (see p. 4), and being flattened out from the first has no opportunity to form radicles.

modifications can still be easily seen; but in others they are at once obscured, incorporated perhaps in the subsequent stock, or, again, in others worn or dissolved off.

The tendency has been to regard the variations at the extreme bases of these Palæozoic corals as accidental, and hence of no real value in classification. This view will, I hope, for the future be abandoned and special attention be paid to any traces which can be seen of the different ways in which the early prototheca was modified. It is quite possible, indeed, that many will be found to have been largely accidental. For instance, such a bend over as that shown in diagram fig. 9 may have been pure accident. The same may be said of radicle formation. More extensive comparisons, especially from this point of view, are necessary before we can say whether such a method of forming a broad base as that shown in fig. 9 became habitual in any group of early corals or not. It is worth noting that other corals are known which adopted it, as, for instance, the *Dipterophyllum glans* of Roemer ('Lethæa Geognostica,' i. p. 371).

More interesting, however, than these irregular, one-sided bendings over are those which took place more or less symmetrically all round. The most perfect of these methods, and, I believe, one of the most recent, is certainly that in which the edge of the prototheca is very early bent down, that is before the cup has any real depth, as already described above (see p. 5) as being the case in the Perforata. The successive bendings down and attempts to bend up again of the edge of this prototheca will, as we have seen, account for the successive wrinkling of the flattened epitheca (see diagram fig. 10). The Perforata owe their leading characteristics to this fact, that upon their flattened prototheca or epitheca a purely septal theca arises, and as the polyps bud the new thecæ are also septal and may mount upwards to form enormous stocks built entirely out of radial septa mutually supported by concentric synaptaculæ, leaving the epitheca, as in *Turbinaria*, as a film beneath the base of the stalk.

On the solution of the question as to when this very early flattening out of the prototheca arose depends that of the first appearance of the Perforata in the coral system. We get what appears to be a flat, very wrinkled epitheca in *Cyclolites* of the Secondary epoch, and again still earlier in the Palæozoic *Palæocyclus*. But an examination of specimens of these at once shows that their flattened epithecæ were not continuous as in fig. 10. In *Palæocyclus* the conditions may be represented by the diagram fig. 11, and for *Cyclolites* by diagram fig. 12, the tabulæ in this latter case being represented internally by vesicular dissepiments *. In these cases, then, instead of there being one continuously expanding prototheca, there was the usual repetition of protothecæ which is so patent in the Palæozoic forms and still persisting, though disguised, in all corals. Even in the Perforata with tall conical septal calicles it must occasionally reappear, while in forms like *Porites* and *Goniopora* it is very marked (see above, p. 9).

These diagrams (11 & 12) are instructive because we see in the Silurian *Palæocyclus* that the original conical shape of the prototheca was not yet quite got rid of but persisted as a kind of stalk, whereas in *Cyclolites* it was quite flattened out. The process of flattening was apparently a slow one, and we may assume that the earlier forms always started from a deep prototheca, however rapidly (as in the case of *Palæocyclus*, for instance) the following protothecæ may have flattened out. Only in time was the flattening-out process so antedated that the very first larval prototheca appeared as a flattened saucer. And then, again, it was necessary to wait for the development of a septal theca to take the place of the flattened prototheca, before the latter could be left to grow outwards continuously as a mere basal support. One factor in bringing about this gradual flattening of the prototheca, as seen, for instance, in *Cyclolites*, might perhaps be seen in the delaying of the secretion of the rigid walls of the cup, which was probably rendered possible in the case of those forms which produced well-developed radial or septal thecæ, the formation of which might, in the early stages, use up the available material †.

There was, therefore, apparently a long period during which the rim of the prototheca was undergoing modification in the direction of bending outwards and, if one may so describe it, a period of uncertainty and hesitation. I am convinced that the gradual steps by which the various flattened

* Tabulæ are secreted when the whole basal skin becomes detached at once and secretes a new continuous floor. Dissepiments are the secretions of portions of the skin coming loose at different times. We may see two reasons for this partial detachment, and, these if correct, would throw some light on the distribution of vesicular dissepiments :—(1) the muscular attachments of the mesenteries buried in the skeleton may hold the skin down at definite spots ; (2) the original floor becomes divided up by radial septa, and thus the skin could not come off in one continuous sheet.

In *Cyclolites* the rims of the tabulæ, the internal parts of which are broken up into vesicular dissepiments, can be traced round the corallum as sharp lines (see fig. 12).

† Lacaze-Duthiers, *l. c.*, found that the septa could be the first skeletal elements produced in developing Perforates, whereas phylogenetically the prototheca came first.

prototheçæ were brought about deserve much more attention than has ever yet been bestowed upon them. While I would not deny that the rise of the radial ingrowths from the inner (or upper) face of the prototheca, that is the septa, on which Milne Edwards's classification is mainly based, may not supply during this period the best taxonomic characters, I still do not think that the variations in the curve of the protothecal rims, or, in other words, the shapes and dispositions of the tabulæ, can be so completely ignored as has hitherto been done. A few examples will show what I mean.

Diagrams figs. 13 *a–f* show some of the forms assumed by the prototheca of adult single Palæozoic corals. They were built up of series of such prototheçæ fitting into one another and usually raised above one another, sometimes by septal folds or ridges, sometimes by vesicular arrangements of the tabulæ of which only the edges showed clear and sharp, or sometimes the sloping sides being vesicular, while the more or less flattened bases are smooth.

It is impossible now to say how far these foldings outwards and downwards of the rims are of the nature of accidental variations. But until we know I can hardly think it right to ignore them so completely as has been done, say, in the genus *Cyathophyllum* as given by Milne-Edwards and Haime. For instance, we find specimens called *Cyathophyllum* which show the prototheca of the shape given in fig. 13 *a* (e. g. *C. turbinatum*, Goldfuss*, said by Milne-Edwards and Haime† to be *C. ceratites*, although they themselves give a figure of it which appears to have the prototheca of the form 13 *h*). Again, Goldfuss (*l. c.* fig. 8 *d*) gives other figures of his *C. turbinatum* with prototheca 13 *c*, while his *C. ceratites* (pl. xvii. fig. 2 *h*) is shown with prototheca 13 *d*, with tabulate floor and vesicular sides. This latter M.-Edwards and Haime called *C. Decheni* with the same form of prototheca as their *C. Bouchardi* ‡. *C. heterophyllum* § appears to have a prototheca of the form, 13 *g*. Goldfuss again gives a *Cyathophyllum helianthoides* (in his pl. xx. fig. 2 *e*) with the same prototheca, 13 *e*, as that given for the genus *Ptychophyllum*.

It is quite true that considerable variation in the slopes of these flattening rims may be expected. For instance, in Goldfuss's figures of *C. helianthoïdes*, just referred to, some have the prototheca 13 *c*, others wih rims even more convex

* Petref. Germ. pl. xvi. fig. 8 *a*.
† Brit. Foss. Corals, pl. 50. fig. 2.
‡ Pol. foss. Terr. paléozoïques, pl. x. fig. 2.
§ Ibid. pl. x. fig. 1.

than 13 *f*. And again variations of curve are seen in the figured section of *Chonophyllum perfoliatum* * with prototheca 13 *b*.

Thus at the very outset we find ourselves face to face with the crux of all systematic work: What is the taxonomic value of these slopes and curves of the rim in any individual case? We know from Mr. Pace's observations † that great variability in the openness and flatness of the calicle can be correlated with the degree of muddiness of the water. The sediment runs more easily off a coral with a flattened open theca than from one with a cup-shaped theca. Then, again, we are justified in assuming that these forms were developed in each case by slow modifications of an originally deep prototheca (age, therefore, may have something to do with the form); and, lastly, we can imagine many different accidents which would tilt or depress such rims.

Nevertheless we have a structure of fundamental importance in the coral skeleton, and the form-variations of this structure may justly claim to take the first taxonomic rank. But how are we to distinguish those of importance from those which are accidental in individual cases? The matter is further complicated in the case of these ancient fossils, because the transition-forms are preserved equally with those which have passed over finally to some well-defined type. It seems fairly clear that classification of such forms must be attempted on wholly different lines from that still in vogue. Before any form receives a name we should satisfy ourselves by a close study of series that it embodies some new principle of structure. Three or four such distinct principles can be gathered from the forms of the prototheca given in Pl. I. diagram 13 *a*–*g*. In *a* the rim continues to show no sharp bend downwards, and is distinct from that in which the rim tends to bend out so as to form an open dish either as 13 *c* or 13 *f*; and both these differ from the sharper curve of the edge all round (13 *g*). Fig. 13 *h*, in which the edge bends rapidly over and then either hangs straight down or shows a tendency to curve up again, seems to me to be very easily distinguishable from 13 *f*, for, even though the two might possibly pass into one another, a smooth curve and a sharp bend are very distinct.

I propose now to leave all but one of these early variations of the prototheca, hoping that I have said enough to claim greater consideration for them in all future work on Palæozoic

* Brit. Foss. Corals, pl. 50. fig. 5. The section perhaps does not run true.

† Ann. & Mag. Nat. Hist. ser. 7, vol. vii. (1901) p. 385.

forms. Fig. 13 *h*, however, is of very great morphological interest and demands some further attention.

In the first place, it shows a simple and very efficient method of enabling the skeleton to stand upright. It differs from the radicle-formation in that the lip bends over all round. The septa which come over the lip run down on the outside just as we know that they run down inside the radicle (see fig. 8 *b*). It is also obvious that the flesh of the polyp must have clothed the outer surface of such a theca, which is no longer the outer surface of the prototheca. To the flesh thus hanging over Bourne's term "perisarc" may be applied, and lower down we will compare it with, and distinguish it from, another principle of structure which also involves the formation of a perisarc. A calicle built up of a succession of such protothecæ as those now under discussion, one fitted inside the other, as in diagram fig. 1, would have a rib-like arrangement of septa running down on the outside; but in this case one would expect to find traces of the hanging rims appearing irregularly one above another as whole or portions of rings round the corallum. They would appear to be drooping or perhaps even show a tendency to curl up again.

It is because no such epithecal rims show in the fig. 2, pl. 50, 'British Fossil Corals,' that I doubt whether its prototheca has this form (13 *h*) or belongs to the type I shall presently describe as also depending upon the formation of a perisarc. This point, then, may be left for the present. It is clear at any rate that its true place is nowhere among the Cyathophyllidæ.

This form 13 *h* is of special importance, however, for the understanding it gives of the morphology of the Silurian *Calostylis* as developed by Lindström.

This coral has been announced as a Palæozoic Perforate, and this claim has had to be dealt with for the British Museum Catalogue, the first section of which, it is proposed, shall deal with the Perforata. As I have shown above, the true Perforates were only possible when the prototheca was flattened out as shown in diagram fig. 10. When thus flattened the septal ridges towered up above it and free of its rim, carrying on the skeleton by themselves alone. The thecæ being constructed solely of radial plates and their synapticulæ were necessarily porous. In *Calostylis* the prototheca was not flattened out at all, but folded as shown in 13 *h*, and the septa were not laminate, but appear to have been represented by a compact mass of large, irregular, rounded or subangular nodules, arranged roughly in radial rows. These come over the edge of the thecal fold and extend down to the rim of the prototheca. The compact layer of septal nodules on both the inner and outer surfaces of the calicles cause the walls to look as if they might be perforated—as if the deep depressions between adjacent nodules might run right through. But this they do not do. One of the chief puzzles of *Calostylis* has been how to explain the pendent tongues of epitheca which hang down irregularly and at intervals round the corallum and sometimes bend even slightly outwards. There can be only one explanation of them, and that is supplied us as soon as we have unravelled the modifications of the prototheca and recognized that its rim was bent in the way shown in this diagram. I repeat it was of importance to have this point settled, for a Silurian Perforate was a difficulty which the British Museum Catalogue had now to dispose of one way or the other.

Turning from this to a somewhat kindred point which has too long been waiting for solution, and which may be partly dealt with in this connexion: Mr. Quelch * has raised the question as to whether the Palæozoic Cyathophyllidæ are not still surviving in the form which he has called *Moseleya*. It is quite true that we have in both cases skeletons built up of the same elements, and at first sight similarly disposed. It has already been pointed out by Mr. Pace that some of the suggested resemblances of *Moseleya* to a *Cyathophyllum* have no value, such as, for instance, the supposed tetrameral symmetry of *Moseleya*. But arguments based upon more or less similarity will not carry us far. The relationship can only be proved or disproved by an analysis of the principles on which the two corals are built. It is not merely the fact that both have similar elements somewhat similarly arranged, which is of importance, but the principles of their respective arrangements. Now whichever of the curves or series of curves of the rim of the prototheca shall afterwards be decided upon as that which shall characterize the genus *Cyathophyllum*, there is no question at all that the special forms which Mr. Quelch relied upon (e.g. *C. Stutchburyi* and *C. regium*, at least as figured by Milne-Edwards and Haime in the 'British Fossil Corals') are of the pattern 13 *d* with the floors tabulate and the sloping sides vesicular. Hence unless *Moseleya* can show a somewhat similar arrangement of tabulæ or vesicles, the relationship between the two cannot be maintained. Now an examination of the available specimens of *Moseleya* shows a principle of protothecal modification which, in some respects, resembles diagram 13 *h*; but on closer analysis it appears to be nearer that other method

* Chall. Report, xvi. 1886, p. 110.

of perisarcal formation referred to above, which will be described in detail in the next section. We shall have therefore to postpone the further discussion of this point for a few pages, contenting ourselves with stating that a comparison of the protothecal specialization of *Cyathophyllum* with that of *Moseleya* shows them to have been well nigh as wide apart as they could possibly be.

One word before leaving these early flattenings of the prototheca as methods adopted by the early Madreporaria for the purpose of retaining the upright position. It is difficult to see how, as single corals, they would be efficient for the purpose unless the rims managed to touch the ground and re-cement a part of the animal to the solid substratum, and this, judging from some of the shapes assumed, does not appear to have taken place. But what is wanted is a closer study of the protothecæ and their earliest modifications. One advantage of early flattening out they would obtain, however; they would grow more slowly in height, and the leverage would not be so great. Further, if this flattening out meant ever so small an increase in the size of the base of the prototheca, we can see that it might be of some value to the coral, even though the rims did not again touch the ground.

The moment these flat-calicled forms begin to bud and form colonies the advantages of the flattening become obvious, as will be seen in another section.

IV. *The Perisarc.*—One of the simplest of the really important methods of keeping the prototheca upright was for the soft parts to bag over all round the cup until they touched the ground, so as to form a secondary fleshy foot. This process differs from that shown in diagram fig. 13 *h*, for it involves no *gradual* bending over of the rim of the prototheca. I assume that the polyp simply overflowed the edge of the cup, that it reached the ground, and even expanded somewhat over the substratum all round the point of attachment of the skeleton. Since the under surface of this overhanging flesh is a continuation of that which secreted the prototheca, it might be expected not only to secrete a layer over the outer face of the cup, but also to deposit a continuation of that layer where it touches the ground. This latter might be thickened to form a solid pedestal, in which the tip of the prototheca would be firmly fixed. The fleshy foot secondarily formed in the way described may have taken almost any shape, even sending out radial prolongations or embracing the round stems of weeds, in which cases the solid pedestals which it secretes would encircle such stems, fixing the corals firmly.

When once fixed the coral may continue to grow in height and size without fear of falling over. If the rise in height is slow the soft parts hanging all round down to the ground may go on thickening the wall, and especially the base, almost indefinitely, so as to keep the corallite nearly cylindrical. In such cases the septal ridges on the inner face of the cup may be continued over the edge as ridges (costæ) or as rows of (costal) spines down the outside. On the other hand, as soon as the base of the prototheca is sufficiently firmly fixed the corallite may grow rapidly in height as well as in width, and in so doing may drag the soft parts away from contact with the ground. The latter will then persist as the typical "*edge-zone*" or "*Randplatte*" round the mouth of the corallite. The withdrawal of the parts that thickened the base while the coral grows in size leads to the latter being turbinate.

From this point of view the typical "*edge-zone*" is in reality a vestigial structure; it is the remains of the perisarc * which in the young stage formed the secondary fleshy foot. But even as such it may continue to fulfil some useful function. It will always continue to leave a layer of skeletal matter on the outer face of the prototheca, thus increasing the thickness and strength of the latter, and it will continue to form costal (=septal) ridges or spines. In *Galaxea* advantage is taken of its gradual withdrawal from contact with the ground to secrete horizontal or arched films round the base of each calicle. In this way the corallites of a *Galaxea* colony are embedded in and supported by an increasingly thick layer of irregular filmy vesicular tissue †.

We are now in a position to reconcile our statement that the epitheca, as usually seen in adult corals, is the rim of the protothecal cup perhaps indefinitely expanded, with the appearances which have led to the text-book statement

* I suggest this distinction between Bourne's "perisarc" and the "edge-zone" of Miss Ogilvie; the edge-zone is the vestigial perisarc. It is important not to confuse the perisarc which hangs over the solid edge of the prototheca with the sides of the polyp of a perforate coral in which the prototheca has been flattened down and the septa alone form a secondary internal theca, and no bagging over of soft parts ever took place.

† There is in the Natural History Museum a specimen showing a group of "*Caryophyllia clavus*" growing on a piece of a telegraph-cable from the Caribbean Sea (700 fath.). The individuals are near together and their perisarcs have covered the intervening spaces with a chalky film. Here and there in the angles made by the corallites with the substratum the film is raised and slopes outward and downward from the sides of the coral. It is this kind of free film formation which has been specialized in *Galaxea*.

that the epitheca is that part of the skeleton secreted by the edge-zone and left on the sides of the coral as it (the edge-zone) is drawn up with the growth of the coral. This secretion may show periodical wrinkles or thickenings if the withdrawal is intermittent; and it is also clearly epithecal, inasmuch as, morphologically, it must be regarded as a doubling over of the rim of the prototheca, as can be gathered from the diagram (fig. 14). But this secretion is only one of many, and, moreover, one of the most highly specialized, modifications of the rim of the epithecal cup. Hence while it is quite correct to call it epitheca, it is quite incorrect to define epitheca in terms of this single specialization of it.

It is also clear that if the term "eutheca" is applied to such cups as those shown in diagrams figs. 1, 2, 4, and 5, in which the lip of the prototheca grows straight on, we want some other term to designate a cup in which the bagging over of the soft parts has practically doubled back the edge of the cup, so that the fold adheres to its sides (see fig. 14). But I would suggest that the simple unmodified theca should be called prototheca, while the term eutheca would be more aptly applied to the theca which has been secondarily attached by a solid pedestal, thickened by the extra matter secreted on its outside, and strengthened and armed by ribs and spines. We might call the wall of *Zaphrentis*, *Streptelasma*, &c. (diagrams figs. 1–4) "continuously protothecate" and that of *Montlivaltia* (diagram fig. 3), or at least of those specimens in which the septa can be seen between the edges of successive saucers, *discontinuously protothecate.*

But although this eutheca, with the meaning just suggested, is due morphologically to a doubling of the wall of the prototheca by the secretion of a layer on the outside of the cup, it can hardly be described as due to a *bending over* of its rim. I conceive of it rather as due to the rapid bagging over of the soft parts, without at the moment any actual continuous growth of the rim. A true bending over would have been a growth process of the rim itself (see fig. 13 *g*). I imagine that only when the soft parts had acquired their new position on the outside of the cup that they commenced secreting the external layer, which is nevertheless strictly a continuance of the rim down the outside and into the basal pedestal.

This explanation of the morphology and origin of the edge-zone throws an interesting light upon a very specialized and morphologically puzzling group, viz. the small highly sculptured free Turbinolidæ. Their origin can now be understood from diagram fig. 14, if we suppose that the powers of secreting carbonate of lime were for some reason restricted, perhaps locally *. In that case the outside fleshy foot might fail to secrete a solid pedestal, and then if, perhaps owing to the movements of the animal itself, the prototheca became detached from the substratum, it would be completely enveloped by the polyp and become a small internal cup-shaped skeleton. The ribs or spines coming over the edge of the cup could then run right down to the extreme tip of the original prototheca, as they do in typical members of the genus. If this origin is correct, the genus *Turbinolia* will have to be regarded as an extreme specialization of the "Euthecate corals," and can hardly, as it now does, give its name to a family.

It is evident then that a considerable reshuffling of the Milne-Edwards classification is required. For instance, as has already been pointed out by Bourne, the "Turbinolidæ" can no longer contain such purely protothecate forms as *Flabellum* and *Rhizotrochus,* while the Euthecate corals will have to include such forms as *Galaxea*, *Euphyllia*, and *Mussa,* which were placed among the Astræidæ by Milne-Edwards and Haime. *Turbinolia* itself will be a specialized offshoot of the Euthecate corals. It would, however, be premature to found such morphological divisions as Protothecata, Euthecata, for it might be discovered, for instance, that the method of forming a perisarcal foot round the larval prototheca has been adopted more than once by different types of coral. Indeed, we seem already to have discovered two ways, viz. that shown in fig. 14 and that found in the Palæozoic *Calostylis* (fig. 13 *h*).

And this brings me back again to the much discussed genus *Moseleya,* already referred to as that which Mr. Quelch, working on a single specimen, took to be a Cyathophyllid. Fortunately Mr. Pace was able to bring more specimens of *Moseleya*, and I have found two others in the great collection made by Mr. W. Saville-Kent on the Great Barrier Reef. All these specimens are *Lithophylliæ.* The only difference that I can detect between them and the 'Challenger' specimen lies in the fact that the latter has flatter and more open calicles. This, as Mr. Pace suggests †, may be merely an adaptation to the mud which we gather is present in the parts where the 'Challenger' specimen was obtained. Examination of the specimens with a view to discover what was the principle of protothecal modification overlying them reveals the type of structure shown in the diagram fig. 15. It is

* They are plentiful in the Barton Clays.
† Ann. & Mag. Nat. Hist. ser. 7, vol. vii. (1901) p. 385.

essentially the same as that shown in fig. 14, but the prototheca was shallow and open and the soft parts had bagged over the low walls on to the ground, doubling them as shown in the figure. Large wing-like septa come over the wall and also reach to the ground or to the rim of the epitheca all round outside. Between these flange-like septa, as they grow upward and outward, the polyps leave one basal secretion after another, so that both inside the cup and outside it there is an increasing thickness of vesicular tissue. In the diagram (fig. 15) the lines are drawn as so many distinct tabulæ. But it would hardly be expected that the successive detachments of the polyp would take place simultaneously within each interseptal loculus, right from the centre of the calicle over the edge of the theca down to the ground. But as dissepiments are only portions of tabulæ, the diagram is the best way of illustrating the facts. This type of structure, in which the vesicular tissue not only rises between the septa within the calicle, but also thickens the column between the costæ outside it, is that which lies at the base of *Lithophyllia*. It is true that emphasis has not hitherto been laid upon this point, for the simple reason that the prototheca had first to be discovered. Milne-Edwards and Haime merely remark that dissepimental tissue is very abundant, while their classing *Mussa* with *Lithophyllia* shows clearly indeed that the arrangement of the dissepimental tissue had not been analyzed. On the other hand Knorr, to whose figure among others Milne-Edwards and Haime refer as a type of *L. lacera*, mentioned the "stony films round the foot" and described the impression made upon him by the words "*new crowns continually covered up the old ones.*" The meaning of this otherwise enigmatical saying is quite clear when we glance at the diagram (fig. 15) here given. We conclude, then, that there is no generic difference between *Moseleya* and *Lithophyllia* and that the genus *Moseleya* is superfluous. At the same time it is due to Mr. Quelch to point out, (1) that the analysis of the essential structure of *Moseleya* was hardly to be discovered from the single specimen at his disposal at the time, and (2) if it had been, there was no existing description of *Lithophyllia* which would greatly have helped him. The calicle of which he made a section was old, very much flattened, and somewhat distorted, and with the tissue on its exposed side largely killed down. This latter point is of great importance, for it is the structure of the sides of the column which is essential to a correct diagnosis. Once, however, the clue is given, which is supplied in abundance by the new specimens, the structure is easy to comprehend.

With the striking superficial resemblance to Cyathophyllidæ to mislead him, it is no wonder that Mr. Quelch was misled. Nor do I see how his claim could have been disproved without a clear understanding of the position of the prototheca in coral morphology.

While on this subject I may point out that Mr. Quelch's figure (*l. c.* pl. xii. no. 5) of a small calicle of *Moseleya* showing marked tetrameral symmetry is seen on the actual specimen to have been distorted by too close contact with the shell of a mollusk much larger than itself. Its internal arrangement is not quite normal. Mr. Pace has presented the Museum with over a dozen specimens, most of them single forms in all stages of growth, and not one shows any such striking tetrameral arrangement. On this subject of tetrameral symmetry in the so-called "Rugose" division of the Madreporaria I would refer the reader to what is said above (p. 11).

Whether, after all, the subsequent classification of the Lithophyllidæ will ultimately admit of the existence of a genus *Moseleya* among them I cannot say. In this paper I am only concerned in showing that it has no place among the Cyathophyllidæ. The latter are characterized by extreme simplicity of protothecal modification, the Lithophyllidæ by great complexity; they are at opposite ends of the evolution of the coral skeleton.

Before closing this section I should like to refer once more to the difference between the principles of modifying the prototheca shown in diagram fig. 13 *k* and diagram fig. 15. In both the soft parts bag over and reach the ground, but in the former the lip grows with the growing of the soft parts and its bend is a true bend. In fig. 15 the soft parts seem to overflow the edge of the cup too rapidly actually to bend the edge. Only after they have taken up their new position do they secrete a layer on the outer side of the cup, and this layer is practically the homologue of the bent-down edge shown in fig. 13 *k*. The two methods are thus clearly distinct, but it is not always easy to say whether a particular case belongs to the one or to the other. For instance, in those specimens of *Lithophylliæ* in the Museum which have the corallites crowded together and forming pseudo-colonies, it is frequently noted that where the interseptal loculi of adjacent corals run into one another the dissepiments are everywhere arched, suggesting an open bend of the thecal lip, such as is shown in the diagram fig. 13 *h*, or even more resembling the bend of fig. 13 *g*, or even of 13 *f*. But in the specimens with single corallites the actual lip of the theca is mostly a solid plate like those shown in diagrams figs. 14 or 15, and from it the dissepiments slope away on the one side into and across the calicle, and on the other down to the substratum. But it is doubtful whether an actual section of the wall would show that structure so straight and continuous as it is shown diagrammatically in the figure (15), and it is quite certain that the tabulæ would not be so regular and complete.

It was some such case as that just referred to (? a specimen of *Acanthastræa*), in which vesicular arched walls separated calicle from calicle, that inspired the diagram given by me on pl. xxxiii. fig. 10 in vol. xxvi. of the 'Journal of the Linnean Society of London.' I am not yet, however, prepared to answer the question as to which of the two methods of edge-zone formation we have just been comparing—that of fig. 13 *h* or of fig. 15—the actual case was due. For, as we have just seen, the *Lithophylliæ* show that the smooth, arched, vesicular dissepimental wall might be a secondary modification, and due to colony formation, of the true edge-zone formation of fig. 14, which is the subject of this section.

V. *Early Budding and Colony Formation.*—In vol. iv. of the 'British Museum Madreporaria,' Introduction, p. 23, I suggested a restricted use of the word "astræiform," viz. to colonies of calicles all reaching to the same height and without any apparent tendency to grow and bud independently. The true astræiform colony is therefore that built up by a calicle which is by habit low and whose buds spread laterally over the substratum all round the parent. The group Astræidæ as now understood consequently cannot be a natural one. It appears to me that we may have astræiform colonies of corals whose protothecæ are modified upon very different plans. And it is on these modifications of this fundamental element that the ultimate classification will have to be based.

We might expect, then, a great development of astræiform colonies among the Palæozoic corals from the forms in which the prototheca was early flattened out in the ways described. We might also expect that it would be those methods of flattening out which were from the first symmetrical, because if the parent had acquired its flattening as a secondary matter, after having perhaps at one time fallen over, it could hardly be expected that the buds would appear with the necessary flattened symmetry straight away, although in some of the Astræid forms with very large calicles this must apparently have taken place.

While I think these conclusions are perfectly justifiable, we learn from the researches of Lindström that one great group of Palæozoic astræiform corals with very small calicles, *e. g.* the genus *Heliolites*, developed from a prototheca which had fallen over. From Lindström's figures * we gather that the lip which touched the ground expanded as a flattened epitheca over the substratum, and buds appeared at intervals upon it. Especially characteristic are the various wrinklings and ridges which appear on the upper face of the epitheca between the buds. As the living layers were periodically detached from and rose above this epitheca they secreted tabulate floors, which repeated its wrinkles and foldings. In this way the structure seen in the section typical of the Heliolitidæ was produced. Through the tabulate laminæ which form the bulk of the coral the calicles run as tubes, while smaller tubes also appear in many cases in the intervening tabulate tissue. These smaller tubes receive their explanation as the continuation of the folds or wrinkles already mentioned through the whole series of tabulæ. Such folds or wrinkles would run as naturally through a series of tabulæ as the septa run apparently continuously through the tabulæ of *Montlivaltia*, as already explained in fig. 3 and p. 8.

If, however, we had had no knowledge of the origin of *Heliolites*, we should have assumed that it had been built up of calicles with the form shown in fig. 13 *j*. And, indeed, this is the form which the calicles of the adult colony assume, but it is not arrived at by a symmetrical outward folding of the rim of the prototheca, but indirectly from a parent the unmodified prototheca of which fell over in the way already described. We owe the small size of the calicle of *Heliolites* to this fact.

The chief difference between the Palæozoic and Recent astræiform corals is due entirely to the more recent development of the radial or septal, as compared with the concentric, protothecal foldings. In Palæozoic times the former were not very pronounced, so that the flattened or curved sides of the protothecal cups with their tabulate floors formed the most characteristic portion of the skeleton. The cup was, however, never quite flattened out, there is always the remains of the bend where the lip first turned over. These bends frequently form ring-folds (see fig. 13 *j*), which become the walls of the fossæ, while tabulæ form not only the floors of these fossæ, but also the areas which intervene between the fossæ. These areas are variously sculptured with radial septa, and when the respective areas of the individual calicles are not marked off from one another, the septa of one may run into the septa

* See K. Sv. Vet.-Akad. Handl. xxxii. (1899), pl. i. figs. 25-28. Compare the case of *Palæocyclus* referred to above.

of those around it, as, for instance, in *Darwinia* and *Phillipsastræa*.

On turning to modern Astræidæ, we find that the tabulate character of the Palæozoic corals has become obscured, on the other hand the septa have become prominent. These conspicuous radial folds of the prototheca make it difficult to discern the exact character of the concentric foldings of the protothecal wall.

I would suggest that, as a rule, the rising of the radial septal folds has also raised the concentric rim-folds. We might diagrammatically express it by imagining a calicle like that in figure 13 *j* becoming changed into the form shown in fig. 16, which represents a calicle with high double walls, and on each side of it a smaller bud. We may assume that the tall ring-fold has been formed at the expense of the earlier horizontal tabulate area round the fossa. It is impossible here to attempt any review of the many Astræid forms, but, speaking roughly, they are built of groups of low calicles with the protothecæ modified in this way. The difference between this and that shown in diagram fig. 14 is that the calicle is shallower and more open.

Without professing any intimate knowledge, I am inclined to believe that most of the different forms now included among the modern Astræidæ may be referred to variations:—

(1) In the distances of the corallites from one another: (*a*) they may be wide apart, as in *Orbicella*, *Solenastræa*, *Echinopora*, &c.; (*b*) they may be close together, *Favia*, *Diploria*, &c.; (*c*) they may be so close that the outer wall of the parent supplies the inner wall of the bud, *Prionastræa*, *Goniastræa*, *Leptastræa**, &c.; (*d*) even these single division-walls may be incomplete, *Hydnophora*.

(2) In the ways the intercalicinal valleys are filled up.

(3) In the characters of the septa and in the way in which they come over the edges of the fossæ and are distributed on the surface of the intervening tissue.

Concluding Notes on the Terminology of the Walls.

A wall built by a direct continuation of the edge of the prototheca should, I think, be called prototheca†. These

* The Palæozoic *Michelinia* might be regarded as the morphological equivalent of these forms before the development of septa disguised the protothecal cups.

† The term epitheca may be retained in its usual sense, and be understood to refer to all traces of the primitive undifferentiated protothecal wall and rim, even though they have lost all signs of having been once parts or expansions of a cup.

primitive protothecal walls, recognized by Miss Ogilvie as equivalent to epitheca, have been hitherto called eutheca. But *proto-* is a more appropriate affix to express primitive simplicity than *eu-*, which better denotes some special excellence. Hence I propose, once more, that eutheca be applied to those walls which have been thickened, ornamented outside, and cemented firmly to the substratum in the way described above (p. 22) and illustrated in diagrams figs. 13 *h*, 14, and 15.

We now come to the term "pseudotheca" of Heider. This is applied to cases in which the septa are so crowded together that they fuse along lines which together constitute a fairly symmetrical solid thecal ring. The parts of the septa within this ring are septa proper and the parts without are costæ. Now I cannot help doubting whether this differs in any respect from the eutheca, for it is obvious that a eutheca, as here understood, over which the septa ran close together, would give exactly the same result.

The suggestion that this wall is built wholly of fused septa does not take the possibility of a ring-fold into account. But from the review of coral morphology here set out it would appear that the ring-fold was a more primitive structure than the radial septa. Further, it is really impossible in a matter of such complicated folds to say how much at their points of crossing belongs to the radial and how much to the concentric elements.

That the concentric element plays a part we gather from the fact that dissepiments frequently slope up the interseptal loculi just as if, had there been space enough, they would mount over the walls. This giving off of dissepiments means that the basal floor shares in the formation of the wall. What is usually called pseudotheca, then, is to my mind simply a modification of the eutheca as here understood, and the word, if retained at all, should have a new significance. My own proposal is to apply it in the sense of Ortmann's "athecalia" *. This term was suggested by that author for the Perforata in which the protothecal cup, being entirely flattened out, a new secondary theca rises up formed entirely out of septa with their synapticular junctions. Now it is obvious that no part of the old protothecal rim is found in this new septate thecal wall, and to mark the total distinction between this and all the wall-formations made by folds of the true lip of the prototheca, it might well be called pseudotheca.

* Zool. Jahrb. (Syst. Abth.) iv. 1889, p. 493.

The term "athecalia" of Ortmann, it may be remarked, has not been very well received, for it is certainly not true that the corallites, say, of *Madrepora* have no thecæ. The very opposite is the case; the thecæ are most pronounced. What we want to express is that these thecæ are morphologically distinct from the original thecæ of the Madreporaria, and no better term could be employed than that here suggested—pseudotheca.

I am aware that a long critique of the views and suggestions of other workers on the subject of the wall should be offered before proposing a revision. But I have the excuse that the revision of the terminology here suggested rests upon a somewhat far-reaching revision of the skeleton. A closer comparison of the terminologies would involve a closer comparison and criticism of the views on the wall-structure of each different author, some of which are, I confess, not always clear to me. Indeed, we seem to have had enough of detailed and complicated discussion. The great want is some simple working hypothesis which will enable us to coordinate the facts.

My own work has convinced me that some order appears out of the chaos if we recognize the prototheca and give it the important place in the morphology of the coral skeleton here all too briefly sketched.

In conclusion, I should like to emphasize the fact that this paper is intentionally devoted to the prototheca and its concentric modifications—that is, to those modifications which alter its cup-shape concentrically. Only occasionally and where necessary reference has been made to the great and complicated system of radial wall-folds which are the most characteristic structures of the stony corals. These have, however, claimed the attention of workers too exclusively in the past. We shall only be able to obtain a true insight into the evolution of the coral skeleton when we understand both systems of modification—the more primitive concentric and the later radial—and can trace out their influences on one another. It is to me a matter of sincere regret that this paper was not published prior to Miss Ogilvie's comprehensive and patient treatise on the septa, for her valuable observations would then, I am convinced, have admitted of more precise and coherent treatment.

EXPLANATION OF PLATE I.

Fig. 1. The three earliest growth-periods of a primitive Madreporarian. The thick basal part is the prototheca (*sens. strict.*), see fig. 2.

The curved line *a* represents the secretion of the basal skin after it has been *dragged* (?) out of the prototheca by the growth of the walls in height; *b* represents the secretion formed by the skin after it has become detached from *a*.

Fig. 2. The same regarded hypothetically as three separate cups, the lowest thick-walled cup being the prototheca (*sens. strict.*); in it cup *a a a* is inserted, and cup *b b b* in *a a a*.

Fig. 3. A diagram to explain the morphology of *Montlivaltia*. The early cups rapidly expand and eventually become a series of saucers, *e e* . ., supported above one another by the septal folds which run continuously upwards. On the right half of the figure the upper part is in section, showing the tabulate floor and the irregularly bent-up rim. On the left half these rims are shown from the outside as irregular bands of epitheca running round the coral.

Fig. 4. An early stage like that of fig. 1, but, having fallen over and resecreted itself at *a*, it bends upwards again. The bagging of the detached basal skins will take the shapes shown, and the fossula in the bases of the cups will be on the convex or dorsal side of the curved skeleton.

Fig. 5. A diagram to show how, if the prototheca proper was wide-mouthed when it fell over, the fossula will come over to the ventral or concave side. *a* is again the spot where the coral secretes a new attachment.

Fig. 6. The diagrammatic representation of the arrangement of the septa in the so-called *Tetracorallia*. It receives a simple explanation as due to the necessary rearrangement of the septa in a coral which fell over and was bending up again. See text, p. 11.

Fig. 7. Diagram to illustrate the method of budding of a prone prototheca and the subsequent bending upwards of parent and buds which might give rise to such a form as *Halysites*.

Fig. 8. Two figures of radicle-formation, after Lacaze-Duthiers.

Fig. 9. Diagram to illustrate the one-sided bend-over of the prototheca such as it is suggested would give rise to the *Zaphrentis gigantea* of Milne-Edwards and Haime. See text, p. 14.

Fig. 10. Diagram to explain the early flattening out of the prototheca in the Perforata. The rim of the cup creeps outwards all round, generally with successive slight bendings up and then down again.

Fig. 11. Diagram of the early stages in *Palæocyclus*. The prototheca proper seems to have fallen over and then suddenly to have widened out, the repetition of this is still more widened out, and so on. What appears to have been a wrinkled basal epitheca is not a continuous growth like that in fig. 10, but a repetition of so many separate protothecal rims.

Fig. 12. Diagram of the early stage of *Cyclolites*. The prototheca is nearly flattened out, but it is still repeated continually, only instead of the secretions of the successively detached skins forming continuous tabulæ, they are broken up into vesicular dissepiments. Here also what appears to be the wrinkled epithecal floor is in reality a concentric series of separate rims.

Figs. 13 *a–g*. Various forms assumed by the protothecæ in Palæozoic corals, all in the direction of becoming flattened out. The developmental transitional stages between the deep prototheca and these adult forms have still in many cases to be worked out.

Figs. 13 *h* and *j*. Two types of foldings of the wall of the prototheca—*h*, seen in *Calostylis*; *j*, common in early astræiform colonies, e. g. *Heliolites*.

Fig. 14. Diagram to show the overflow of the prototheca by soft parts which bag all round down to the ground and form a new fleshy foot. This secretes a pedestal which can fix the prototheca firmly to the substratum and doubles the thickness of the protothecal wall. This, it is suggested, should be called the *eutheca*.

Fig. 15. Diagrammatic section of a *Lithophyllia*. Large wing-like septa radiate out over the wall, and dissepiments are formed on both sides of it; within the calicle they slope inwards, on its outer side they bend down and thicken the column with vesicular tissue between the costæ. Mr. Quelch's genus *Moseleya* is built on this plan, and cannot therefore be a Cyathophyllid with prototheca modified on one of the simpler plans shown in figs. 13 *a–f*.

Fig. 16. A diagram to illustrate the principle of structure characterizing the modern Astræidæ: 1 is the central parent calicle with the prototheca modified somewhat as in fig. 14; 2, 2 represent buds from the lateral edges, the budding thus resulting in the production of an astræiform colony.

II.—*Some Parasitic Bees.* By T. D. A. Cockerell.

Cœlioxys ribis, var. *Kincaidi*, n. var.

♀.—Length 11–13 millim., the difference in size partly dependent on the extension or retraction of the apical part of the abdomen.

Similar in all structural characters to *C. ribis*, but the pubescence of the head and thorax is ochreous, the basal part of the third abdominal segment is more sparsely punctured, and the apical dorsal plate has the apex beyond the slight lateral constriction a little more produced. There are distinct and conspicuous transverse grooves across the middle of the second and third abdominal segments, but not on the fourth or fifth. Tibial spurs black.

Hab. Olympia, Washington State, June 9 to 24, 1895, June 26, 1896, five females (*T. Kincaid*).

This is the first *Cœlioxys* recorded from the north-west. It is quite different from *ribis* in appearance, but structurally it is almost the same, having the same sculpture on the penultimate ventral segment, &c. A male collected by Mr. Kincaid at Olympia, June 18, 1895, is presumed to belong to *C. ribis Kincaidi*, though the pubescence (especially on the face) is white. This male almost exactly agrees with